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Assessing the impacts of the introduced channel catfish *Ictalurus punctatus* using the Comparative Functional Response approach

Abstract

In the metric “Relative Impact Potential” (RIP), the functional response (FR) of a non-native species can be compared to that of a native analogue and combined with the species abundance to predict its environmental impact. Here, using the River Guaraguaçu (Brazil) as a case study, this methodology was implemented to identify the impacts of the non-native channel catfish *Ictalurus punctatus* compared to a native species *Rhamdia quelen* towards small prey fish. Both species exhibited Type II FRs, however handling times were lower for *I. punctatus*, resulting in a greater maximum feeding rate in this species. Consequently, an $RIP > 1$ was found, indicating that *I. punctatus* represents a superior impact to prey when compared to its native analogue. These results demonstrate that *I. punctatus* is a potential threat to small endangered fish species. Therefore, policies to avoid escapes from aquaculture should be created and the abundance of *I. punctatus* controlled.

Keywords

alien species, aquaculture, fish, freshwater, management, Relative Impact Potential

1 Introduction

The introduction of non-native species to novel regions is one of the main drivers of species extinction and is considered the second major cause of global biodiversity loss after habitat destruction (Bellard, Cassey & Blackburn, 2016; Clavero & García-Berthou, 2005; Vitousek, D'Antonio, Loope & Westbrooks, 1996). Predation by non-native species can devastate native prey populations as non-native predators are often more efficient consumers of resources compared to their native counterparts (Paolucci, MacIsaac & Ricciardi, 2013; Salo, Korpimäki, Banks, Nordström & Dickman, 2007; Simberloff & Vitule, 2014). Compounding this, native prey often do not exhibit effective anti-predator behaviour due to a lack of shared evolutionary history with the new predator (Cox & Lima, 2006). These mechanisms can explain the establishment success of non-native predators and their negative impact in the recipient community (Gallardo, Clavero, Sánchez & Vilà, 2016; Latini & Petrer, 2004; Sharpe, De León, González & Torchin, 2017; Simberloff et al., 2013; Trumpickas, Mandrak & Ricciardi, 2011).

Prediction and quantification of impacts of non-native species is of great importance for conservation of biodiversity, although there is no agreed standard methodology for doing so (Kumschick et al., 2015; Parker et al., 1999; Ricciardi, Hoopes, Marchetti & Lockwood, 2013). The comparative functional response (CFR) has been proposed as an approach that “can unify invasion ecology” (Dick et al., 2017a), providing a trait-based methodology for measuring resource-use interactions of non-native species as a means of predicting their potential ecological impact. The CFR approach is based on the comparison of the functional response (FR) of non-native and trophically analogous native species, where the difference in the magnitude of the FR can predict and quantify the relative impacts of the non-native species (Dick et al., 2014).

A FR is defined as the relationship between consumption rate and resource density (Holling, 1959b). There are three types of FR: Type I – an increasing linear relationship between resource density and consumption until a threshold of satiation; Type II – a decelerating rate of consumption that reaches an asymptote at higher densities; and Type III – an S-shaped curve where the consumption rate first accelerates at low densities and then decelerates towards satiation (Holling, 1959b). The FR type of the predator can have direct effects on the stability of the prey population, for instance Type II FR has destabilising effects with high consumption at low densities, whereas Type III has stabilising effects with a refuge of predation at low densities (Oaten & Murdoch, 1975; Sinclair et al., 1998). As FRs measure the *per capita* effect of a non-native species, it can be combined with the abundance of the species in the field, in a metric called the Relative Impact Potential (RIP), to enhance the predictive power of this approach (Dick et al., 2017b).

A native to North America, the channel catfish (*Ictalurus punctatus* Rafinesque, 1818) has been introduced worldwide for aquaculture and sport fishing purposes (CABI, 2019). The species was first introduced in Brazil in 1971 and, having potentially escaped accidentally from aquaculture cages (Orsi & Agostinho, 1999; Welcomme, 1988), it is now widely found in Brazilian water bodies (Cruz-Spindler et al., 2012; Ota, Message, Graça & Pavanelli, 2015; Zanatta et al., 2010). As a non-native species, *I. punctatus* is a potential threat to local fish assemblages through competition and predation of native species (e.g. Matsuzaki et al., 2011; Townsend & Winterbourn, 1992; Troca & Vieira, 2012). For example, the decline and extinction of species, such as the razorback sucker *Xyrauchen texanus*, in communities invaded by *I. punctatus* has been reported (CABI, 2019). Additionally, *I. punctatus* demonstrates high rates of dispersal, which is aided by its ability to adapt to a wide range of habitats (Olden & Poff, 2005).

The aim of the present study was to apply the CFR approach and the RIP metric to assess the potential impacts of the invasive *I. punctatus* in a highly-diverse river in Brazil, the River Guaraguaçu. The abundance of the species is not constantly monitored, but there are reports about the establishment of this species in the river basin, as well as, in other basins of the Paraná State (Vitule, Umbria & Aranha, 2005; Vitule, 2008). Based on the species traits and invasion history of *I. punctatus* (Gutierre, Vitule, Freire & Prodocimo, 2014; Tatarenkov, Barreto, Winkelman & Avise, 2006; Townsend & Winterbourn, 1992; Wellborn, 1988), and considering its taxonomic distinctiveness within the recipient community (Ricciardi & Atkinson, 2004), the likely impact of *I. punctatus* on native species and ecosystems is through an elevated consumption of small stream fishes.

To address the paucity of research on non-native species impacts in South American countries (Bellard & Jeschke, 2016; Speziale, Lambertucci, Carrete & Tella, 2012; Vitule, Freire, Vazquez, Nuñez & Simberloff, 2012), the present study aims to enhance the understanding of the impacts of introduced predators in the Neotropical region, where biodiversity is both rich and threatened (Lowry et al., 2013; Myers, Mittermeier, Mittermeier, da Fonseca & Kent, 2000).

2 Methods

2.1 Species used

Ictalurus punctatus is a nocturnal forager that uses a variety of habitats with preference for shallow warm waters (Bayley & Harrison, 1948; Braun & Phelps, 2016; Jordan, Neumann & Schultz, 2004), detecting food using olfactory and visual cues (Becker, 1983). Young *I. punctatus* feed mainly on insects, but adults are usually omnivorous and prey also on fish (Bailey & Harrison, 1948; Braun & Phelps, 2016; Hill, Duffy &

Thompson, 1995; Tyus & Nikirk, 1990). The species has opportunistic behaviour and is generalist, preying on a wide range of available resources in non-native regions (Endo et al., 2015; Haubrock et al., 2018).

The FRs of the non-native channel catfish *I. punctatus* were compared to a native consumer, the South American silver catfish *Rhamdia quelen* (Quoy & Gaimard, 1824), which is a benthic species widely distributed in lakes, reservoirs and rivers of Central and South America (Gomes, Golombieski, Gomes & Baldisserotto, 2000; Silfvergrip, 1996). There are few studies on the biology of *R. quelen*, which like *I. punctatus* is representative of the Siluriformes and is generally described as nocturnal and omnivorous when mature (Bailey & Harrison, 1948; Gomes et al., 2000; Goudie, Davis & Simco, 1983). Adults of *R. quelen* are considered generalists, feeding on fish, crustaceans, insects, vegetation and organic detritus (Guedes, 1980; Meurer & Zaniboni Filho, 1997). *Ictalurus punctatus* and *R. quelen* have many similarities in their anatomic digestive systems and diet (Piedras, Pouey & Moraes, 2006) which make *R. quelen* an appropriate resident comparator for *I. punctatus* in the FR experiments described here.

Both species also spawn in the spring, with temperature an important factor in reproduction (Becker, 1983; Gomes et al., 2000). *Rhamdia quelen* has low fecundity rates and do not present parental care (Gomes et al., 2000). Females of *I. punctatus* have around 8,000 eggs per kg body weight and males guard the eggs during a period of incubation of 5 to 10 days (Becker, 1983). *Ictalurus punctatus* reaches sexual maturity at 300–375 mm in total length (TL), whereas *R. quelen* generally matures at 134–175 mm TL (Gomes et al., 2000; Jackson, 2004; Shephard & Jackson, 2005).

Blue tetra *Mimagoniates microlepis* (Steindachner, 1877), a congeneric of the locally and nationally threatened *M. lateralis* (Abilhoa & Duboc, 2004; Rosa & Lima, 2008; MMA, 2014), is abundant in natural water bodies and was used as prey in

experimental trials. Both *Mimagoniates* species are sympatric and are representatives of Glandulocaudinae, which is characterised by small stream fishes (Braga, Braga, & Vitule, 2013; Menezes & Weitzman, 2009). *Mimagoniates lateralis* is the smallest species of the genus, reaching maximum 40 mm standard length (Menezes & Weitzman, 2009; Rosa & Lima, 2008).

2.2 Experimental design

For the experimental protocol (Figure S1), which was approved by the Ethics Commission on the Use of Animals of the Biological Sciences Department of the Federal University of Paraná (CEUA/BIO UFPR – Certificate nº1027), juveniles of predator fish species (*I. punctatus* and *R. quelen*) were obtained in local aquaculture farms and stored in tanks of 300 L in the lab. Each species was kept in a different tank with constant aeration and filtration for acclimation during 30 days. Prey fish were collected in the field using fishing nets and kept in an 80 L aquarium, with constant aeration and filtration, and were also acclimated for 30 days. The temperature in the lab was kept at 22–26°C under a natural light regime. During the acclimation period predators were fed every 48 h with sausage to standardise prior experience.

Experiments were performed in 10 L opaque plastic boxes (35 × 20 × 25 cm) with constant aeration. Individuals of predator species were randomly selected one day prior to use and placed in the experimental aquariums for 24 h acclimation. Predators ($n = 9$ per species) were size-matched with respect to total length (*R. quelen*: 16.39 cm \pm 1.15 and *I. punctatus*: 16.83 cm \pm 2.14; Students' *t*-test, $t = -0.55$, $df = 16$, $p = 0.59$). Each predator specimen was reused in two more trials with different initial densities. After the acclimation period, they were held without food for 72 h to standardise hunger levels. Predators were then presented with the prey at five initial densities (2, 5, 10, 20, and 30 individuals), with five replicates per density. Prey were also size matched with respect to

total length by visual selection (≈ 3 cm). Experiments were initiated at 14:00 and prey consumption was recorded after 24 h. Controls were three replicates of each initial density of prey in the absence of predators.

2.3 Data analysis

The FR type was determined from a logistic regression of prey density by the proportion of consumed prey, as proposed by Juliano (2001). A negative first order term indicates a Type II FR, whereas a positive first order term followed by a negative second order term indicates a Type III FR (Pritchard, Paterson, Bovy & Barrios-O'Neill, 2017). The FR curves and the parameters attack rate (a) and handling time (h) were modelled using Maximum Likelihood Estimation (Bolker, 2008) with the Rogers' (1972) random predator equation that considers the depletion of prey without replacement along the experimental period:

$$N_e = N_0 \{1 - \exp [a (N_e h - T)]\} \quad (1)$$

where N_e is the number of prey consumed, N_0 is the initial density of prey, a is the attack rate, h is the handling time and T is the experimental period, given in days. The attack rate (a) is the instantaneous capture rate, *i.e.* the rate at which the consumer encounters resource items per unit of resource density; and the handling time (h) is the time spent capturing and consuming the prey item (Brose, 2010; Holling, 1959a; Jeschke, Kopp & Tollrian, 2002). The h was used to estimate the maximum feeding rate ($1/hT$), which represents the FR curve asymptote. To compare the FR of each species, the parameters a and h were compared between predators using the indicator variables method, as the following equation:

$$0 = N_0 - N_0 \exp \{[a + Da(j)] [h + Dh(j)] (N_e) - T\} - N_e \quad (2)$$

where j is an indicator variable that takes value 0 for *R. quelen* and 1 for *I. punctatus*. The parameters Da and Dh estimate the differences between the predators in the value of the parameters a and h , respectively. If these parameters are significantly different from zero, then the two species differ significantly in the corresponding parameters (Juliano, 2001). To visualise the uncertainty around the fitted functional responses, 95% confidence intervals were constructed by bootstrapping ($n = 2000$) data around FR curves. If confidence intervals do not overlap, then it can be stated that species FRs differ (Paterson et al., 2015). Analyses were carried in R v. 3.4.1 (R Core Team, 2015) using the ‘frair’ package (Pritchard et al., 2017) at 0.05 significance.

The Relative Impact Potential (RIP) metric was calculated using the following equation, according to proposed by Dick et al., 2017b:

$$RIP = \frac{FR_{\text{non-native}}}{FR_{\text{native}}} \times \frac{AB_{\text{non-native}}}{AB_{\text{native}}} \quad (3)$$

where FR is the estimated maximum feeding rate ($1/hT$) and AB is the field abundance/biomass of the species. When $RIP < 1$, the non-native species is predicted to have less impact than the native equivalent; when $RIP = 1$, there is no impact above that driven by native equivalents; whereas $RIP > 1$ indicates a likely non-native ecological impact (Dick et al., 2017b). Data of total abundance and biomass were taken from literature, from samples collected in River Guaraguaçu using a variety of fishing gears (Vitule, 2008) (Table S1). As data from different methods of capture and of different fishing efforts were compiled (Table S1), the capture per unit effort (CPUE) was calculated to standardise these differences. This was the number of fishes captured divided by the number of fish hooks or area of gill nets, multiplied by fishing effort in hours.

3 Results

None of the prey fish died in any of the control replicates, therefore prey mortality in the experimental trials was attributed to predation. Both species obtained a negative first-order term from logistic regressions, indicating a Type II FR (Table 1, Figure 1). Parameter estimates of the FR model were all statistically significant (Table 1). The attack rate did not differ between species ($Da = -0.646$, $z = -0.447$, $p = 0.655$), but the handling time was significantly lower for *I. punctatus* ($Dh = 0.053$, $z = 2.209$, $p < 0.05$), and thus a higher maximum feeding rate was obtained (Table 1).

The RIP calculated using field data on total abundance did not demonstrate a greater impact of the non-native species ($RIP < 1$, Table 2). Considering biomass, the impact of *I. punctatus* was found to be similar to the native species *R. quelen* ($RIP \approx 1$, Table 2). However, using CPUE data, *I. punctatus* was found to have a greater impact ($RIP > 1$, Table 2).

4 Discussion

Both predator species in the present study demonstrated a Type II FR when exposed to *M. microlepis*. Most, if not all, of the prey were consumed at low densities, which suggests that in open waters this could lead to destabilising effects on the local population (Holling, 1959a; Murdoch & Oaten, 1975; Sinclair et al., 1998). A Type II FR may therefore pose a greater concern in open waters, where endangered, such as *M. lateralis*, are often found to exist in small populations (IUCN, 2012; Sinclair et al., 1998).

The CFR approach provided evidence that *I. punctatus* is likely to exert an ecological impact to native small fish prey, and it is possible that other small-bodied endangered fish species suffer predation pressure from *I. punctatus* in a similar manner as *M. microlepis*. Despite the overlap of FR curves of *I. punctatus* and its native comparator *R. quelen* (Figure 1), the results of the present study suggest that *I. punctatus*

exerts a greater predation pressure on *M. microlepis*, with a significant lower handling time, and therefore a higher maximum feeding rate. Lower h and consequently higher $1/hT$, due to faster rates in processing prey, can explain the superior impact of invaders (Alexander, Dick, Weyl, Robinson & Richardson, 2014). The lower handling time of *I. punctatus* (Table 1) may be due to differences in the resource acquisition ability of the species (Alexander et al., 2014). *Ictalurus punctatus* has taste buds across its body and within its barbels, which aid in perception of food and trigger feeding behaviour (Caprio et al., 1993; Valentincic & Caprio, 1994). *Ictalurus punctatus* also has relatively larger eyes than other siluriform catfishes, which may facilitate visual predation in clean waters, such as of the experimental conditions (Davis, 1959). The similar FRs of *I. punctatus* and *R. quelen* towards the prey (Figure 1) also suggest that these species may have niche overlap, resulting in either resource competition or repartition in open waters. Both species seems to use the same strategy to find resources, as their barbels are sensitive to amino acids or hydrolysed proteins, which triggers feeding behaviour (Caprio, 1975; Broggi, 2014).

Ictalurus punctatus are less abundant than native *R. quelen* in the River Guaraguaçu, which suggests a lower relative predation impact than the native species. However, using standardised CPUE data, a different result emerged, with *I. punctatus* presenting a higher abundance (Table 2), and therefore a potentially greater impact than *R. quelen*. Using only the FR provides a modestly-powered predictor of non-native species impacts, because a low FR can be compensated by high abundance in the field (Lavery et al., 2017). The results obtained here, of a greater RIP using CPUE field data (Table 2), are sufficient to justify the need of management and control of *I. punctatus* population. Early interventions may be successful in avoiding non-native species impacts

(Simberloff, 2003), and in the present case, the results provide evidence to motivate the immediate action to manage *I. punctatus* at low population levels.

Propagule pressure is widely believed to play a fundamental role on the successful establishment and permanency of non-native species, contributing to its continuous impact (Copp, Templeton & Gozlan, 2007; Kolar & Lodge, 2001; Ruesink, 2005). The juvenile *I. punctatus* used in these experiments were obtained from local aquaculture, which is recognised as the major pathway of introduction of *I. punctatus* and other freshwater invasive species (CABI, 2019; Casal, 2006; Gozlan, 2008; Naylor, Williams & Strong, 2001). *Ictalurus punctatus* is among the most cultured freshwater fishes globally, and its global total production in 2016 reached 432,932 tons (FAO, 2018). There are many fish-farms in Paraná State that cultivate and sell young-of-the-year *I. punctatus* despite a legislation that classifies this species as Category I, which has its “transportation, breeding, release or translocation, cultivation, propagation, commercialization, donation or intentional acquisition prohibited by any means” (Environmental Institute of Paraná, 2015). Despite this, the production of *I. punctatus* continues to increase, and the risk of escapes from aquaculture ponds is a constant threat in Neotropical streams, contributing to a high propagule pressure (Forneck, Dutra, Zacarkim & Cunico, 2016; Lima Junior, Pelicice, Vitule & Agostinho, 2012; Vitule, Freire & Simberloff, 2009). This failed attempt to ban the introduction of *I. punctatus* in Paraná could be responsible for the declines in status of many endemic fishes (Lima Junior et al., 2018; Pelicice et al., 2017; Vitule et al., 2009). Therefore, the cultivation of the *I. punctatus* should be avoided in Paraná in order to reduce its spreading into natural water bodies.

Besides constant introductions of *I. punctatus*, the species’ reproductive behaviour (guarders, nest spawners) is more specialised than that of *R. quelen*

(nonguarders, open substratum spawners) (see Balon, 1975). The male *I. punctatus* guards the eggs until they hatch, a feature that may favour the establishment of the non-native species in the field (Marchetti, Moyle & Levine, 2004; Tatarenkov et al., 2006). Also, predation of *I. punctatus* by native fishes in the study region is unlikely due to the dorsal and pectoral spines of *I. punctatus* (Bosher, Newton & Fine, 2006).

In the present study, juveniles of similar body size were used, which contrasts natural populations. Predator body-size influences most aspects of feeding behaviour and there are allometric relationships between body size and the FR parameters, with increases in a and decreases in h as predator size increases (Brose, 2010; González-Suárez et al., 2011; Miller, Crowder, Rice & Binkowski, 1992; Vucic-Pestic, Rall, Kalinkat & Brose, 2010). In the case of the two study species, *I. punctatus* can reach larger adult sizes than *R. quelen*, as the first can be mature at size 300 mm TL and *R. quelen* is already mature at 175 mm TL (Gomes et al., 2000; Jackson, 2004; Shephard & Jackson, 2005), which may lead to an increased *per capita* effect of the non-native species that could influence the FR results.

As with many fishes, the degree of piscivory tends to increase in *I. punctatus* with increasing body length (Starostka & Nelson, 1964). As juveniles were used here, it can be expected a greater *per capita* effect of adults of in the field. Furthermore, omnivores like *I. punctatus* tend to present a Type II FR when exposed to a single type of prey, and the presence of an alternative food source may therefore affect our results (Médoc, Thuillier & Spataro, 2017; Murdoch & Oaten, 1975). Indeed, alternative food availability has been shown to change FRs of amphipods, killer shrimp *Dikerogammarus villosus* and the freshwater shrimp *Gammarus pulex*, with the superior consumption of the invasive *D. villosus* disappearing when it was presented with an alternative non-animal food (Médoc, Thuillier & Spataro, 2017).

Differences in predator biomass also likely strengthen the impact of *I. punctatus*.

The mean biomass of *I. punctatus* specimens captured in the River Guaraguaçu was more than twice of the native species and the RIP using biomass was ≈ 1 (Table 2), which suggests that the impact of *I. punctatus* in the wild is greater than the native predator despite its lower abundance. Neither predator species nor size alone can predict consistently the FR type and its associated parameters, so both predator identity and size should be considered to assess fully the potential ecological impacts of a non-native species on invaded communities (Anderson, Linares, Dodson & Semlitsch, 2016; Guo, Sheath, Amat Trigo & Britton, 2016).

It is important to consider other factors that may alter FR results, such as habitat complexity (Alexander, Dick, O'Connor, Haddaway & Farnsworth, 2012; Barrios-O'Neill, Dick, Emmerson, Ricciardi & Macisaac, 2015), which in some cases can change the FR type and parameters. This can occur if habitat complexity acts as a refuge for prey in low density (Alexander, Kaiser, Weyl & Dick, 2015) or contributes to predation of ambush predators, resulting in a higher consumption rate (Santos, García-Berthou, Hayashi & Santos, 2013). This context-dependency factor may also be an important feature to be tested in the FR of *I. punctatus*, as the River Guaraguaçu has been invaded by the African signalgrass *Urochloa arrecta*, a macrophyte that increases habitat complexity (Michelan, Thomaz, Mormul & Carvalho, 2010; Thomaz & Cunha, 2010; Vitule, Umbria & Aranha, 2006).

To quantify and predict the impacts of non-native species is of fundamental importance to conservation efforts, because such data are needed in order to create plans for management and control of damaging species. The CFR approach and the RIP metric have been shown as an effective tool for predicting the impact of existing and emerging high impact non-native species and can be performed elsewhere in a very simple fashion

(Alexander et al., 2014; Dick et al., 2017a, 2017b; Laverty et al., 2017). Therefore, the CFR approach is of particular usefulness in both developing and developed countries because data on non-native fish impacts are lacking for most species. Whereas, data on non-native species impacts are even more scarce in less developed regions, where the number of potentially threatened endemic species is often high (Frehse, Braga, Nocera & Vitule, 2016; Lövei, Lewinsohn & Network, 2012; Nuñez & Pauchard, 2010; Vitule et al., 2017).

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Figure legend

Figure 1. Type II Functional Response curves for channel catfish *Ictalurus punctatus* (dashed line) and South American silver catfish *Rhamdia quelen* (solid line) preying on blue tetra *Mimagoniates microlepis*. Points indicate mean consumption per density. Shading represents bootstrapped ($n = 2000$) 95% confidence intervals for each species.

Assessing the impacts of the channel catfish *Ictalurus punctatus* using the Comparative Functional Response approach

Table S1. Field data on total abundance (n), capture per unit effort (CPUE) and total biomass (in grams) of channel catfish *Ictalurus punctatus* and South American silver catfish *Rhamdia quelen* captured in 17 standardised samples, between 2005 and 2007, using different fishing gears. Data from Vitule (2008). Long lines were of 10 m length, and gill nets were of 30×1.70 m, with exposure times in all cases being 1500 hours.

Fishing gear (and mesh size)	Effort	n	CPUE	Biomass (g)
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<i>Ictalurus punctatus</i>					
Longline	3 longlines with 10 fish hooks	8	0.000178	9312	
Gill net (20 mm)	Gill net	5	6.54E-05	1069	
Gill net (40 mm)	Gill net	4	5.23E-05	2075	
Gill net (60 mm)	Gill net	1	1.31E-05	740	
Fishing rod	4 anglers, \approx 60 h	$\frac{1}{2}$	0.05	14496	
<i>Rhamdia quelen</i>					
Longline	3 longlines with 10 fish hooks	40	0.000889	14106	
Gill net (20 m)	Gill net	31	0.000405	8133	
Gill net (40 mm)	Gill net	33	0.000431	14768	
Fishing rod	4 anglers, \approx 60 h	8	0.033333	1978	

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642